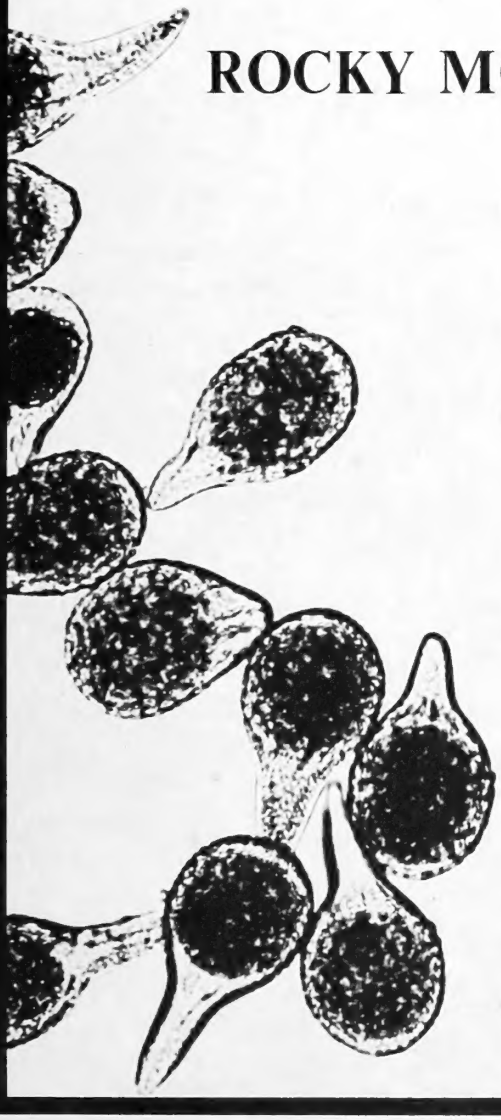
CRONARTIUM COMANDRAE IN THE ROCKY MOUNTAIN STATES

by
R. G. KREBILL



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RECENT PUBLICATIONS ON STEM RUSTS OF HARD PINES BY INTERMOUNTAIN FOREST AND RANGE EXPERIMENT STATION

Koenigs, J. W. 1966. An evaluation of antibiotics for control of comandra rust on lodgepole pine. Plant Dis. Reptr. 50: 528-531.

Krebill, R. G. 1965. Comandra rust outbreaks in lodgepole pine. J. Forest. 63: 519-522.

Krebill, R. G. 1968. Histology of canker rusts in pines. Phytopathology 58: 155-164.

Laycock, W. A., and R. G. Krebill. 1967. Comandra, grazing, and comandra blister rust. U. S. Forest Serv. Res. Pap. INT-36, 9 pp.

Mielke, J. L., R. G. Krebill, and H. R. Powers, Jr. 1968. Comandra blister rust of hard pines. U. S. Dep. Agr., Forest Serv., Forest Pest Leafl. 62.

Mielke, J. L., and R. S. Peterson. 1967. Albino *Peridermium harknessii* in ponderosa pine. Plant Dis. Reptr. 51: 306-309.

Peterson, R. S. 1966. *Cronartium* mycelium parasitizing gymnosperm and angiosperm tissues simultaneously. Mycologia 58: 474-477.

Peterson, R. S. 1966. Limb rust damage to pine. U. S. Forest Serv. Res. Pap. INT-31, 10 pp.

Peterson, R. S. 1966. On sweetfern blister rust. Plant Dis. Reptr. 50: 744-746.

Peterson, R. S. 1967. The *Peridermium* species on pine stems. Bull. Torrey Bot. Club 94: 511-542.

Peterson, R. S. 1968. Limb rust of pine: the causal fungi. Phytopathology 58: 309-315.

Peterson, R. S., and R. S. Quinard. 1967. *Cronartium conigenum*: distribución y efectos en los pinos. Boletin Tecnico 19, 11 pp.

Peterson, R. S., and R. G. Shurtleff, Jr. 1965. Mycelium of limb rust fungi. Amer. J. Bot. 52: 519-525.

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CONTENTS

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INTRODUCTION

Cronartium comandrae Pk. is a heteroecious fungus that lives as an obligate parasite in hard pines and comandras. Although distributed across North America, *C. comandrae* is probably most common now in the Rocky Mountain States. There it produces uredinia and telia on *Comandra umbellata* (L.) Nutt. ssp. *pallida* (A. DC.) Piehl (fig. 1) and aecia on lodgepole pine (*Pinus contorta* Dougl.) and ponderosa pine (*Pinus ponderosa* Laws.). On pine it produces the destructive canker disease (fig. 2) known as comandra blister rust (Hedgcock and Long 1915 and Mielke 1961). This rust was believed to be an important problem in the West only on ponderosa pine until Mielke (1957) reported that it was also causing widespread damage to lodgepole pine in the Rocky Mountains. Concern developed that the rust was intensifying and could become a serious obstacle to the orderly management of lodgepole pine. Subsequent studies of the chronology of comandra blister rust outbreaks in the Rocky Mountain States, made by dating cankers by ring analysis, indicated that infection of lodgepole pine was abundant for several decades prior to about 1945, and since then extremely scarce (Peterson 1962 and Krebill 1965). Thus the comandra blister rust damage that is now apparent in lodgepole pine in the Rocky Mountain States arises from old outbreaks of infection and will not increase unless future outbreaks occur. To better evaluate the potential threat of this rust, we must have a thorough understanding of the causes of outbreaks.

It has long been suspected that fluctuations in the abundance of comandra might influence the occurrence of comandra rust outbreaks in pine. Meinecke (1928) indicated that such changes were major factors regulating outbreaks in ponderosa pine. Some evidence was provided by a severe outbreak of comandra rust in the Shasta River drainage of northern California. When the site was examined in 1914 by J. S. Boyce, heavily infected comandra occurred commonly among recently infected ponderosa pine (Wagener 1960).[1] In the same area nearly 50 years later Wagener (1960)[1] found that the rust was still common, but both comandra and young cankers in pine were scarce.

In the Rocky Mountain States fluctuations in comandra populations are poorly documented. Mielke (1957) suggested that changes in comandra abundance might be occurring in the Intermountain area, and Laycock and Krebill (1967) present some evidence of change in long-term study plots. Also, the fact that it is now difficult to find comandra near some areas where old pine infections are abundant (Peterson 1962 and Krebill 1965) indicates reduction of comandra, unless the infections were due originally to long-distance spread of the rust.

The causes of changes in abundance of comandra are even less well known than the influence of such changes. Wagener (1960)[1] suggested that closing of an overstory might have reduced comandra in the Shasta River drainage outbreak area. This idea has merit since comandra does not survive in deep shade. Meinecke (1928) suggested that continual infection of comandra over a number of years following a buildup of comandra rust in pine causes comandra populations to decline and remain at low levels until the rust dies down in pine; then comandra can reestablish itself and set up conditions for new waves of pine infection. This sequence of events might occur on sites where comandra is not a stable member of a community. However, comandra is commonly abundant now near most old outbreak areas in the Rocky Mountain States, despite frequent heavy infection of the plants. The suggestion has also been made that comandra has increased in the West because of overgrazing (Kimmey 1958 and Mielke 1957 and 1961), but a more recent evaluation casts doubts on this idea (Laycock and Krebill 1967).

Although presence of the alternate host is a requirement for spread of the rust, climatic conditions suitable for infection and development also play a large part (Wagener 1960,[1] Mielke 1961, Krebill 1965, and Powell 1965). The present study improves our understanding of this phase of the epidemiology of comandra blister rust in lodgepole pine by revealing the influence of some physical factors of the environment on the life cycle of *C. comandrae* and by relating these findings to the phenology of the hosts and parasite in a portion of the Rocky Mountains.

[1] *Wagener, W. W. Sporadic diseases in young stands in California and Nevada. Pp. 14-22. IN: Proc. of the Eighth Western Int. Forest Dis. Work Conf., Nov. 29-Dec. 2, 1960. Unpublished; permission to cite granted by W. W. Wagener.*

Figure 1.– *Comandra umbellata* ssp. *pallida*, host plant for the uredinial and telial stages of *Cronartium comandrae* in the Rocky Mountain States.

Figure 2.– *Cronartium comandrae* canker in lodgepole pine in Custer National Forest, Montana. Bark was removed by rodent chewing, as is typical in the West.

SPORE VIABILITY AND GERMINATION

To explore the influence of environmental conditions on spores during dissemination and germination, many experiments were run under controlled and monitored environmental conditions. Experiments were made to investigate all spore stages involved in infection of comandra and pine, that is (1) aeciospores on pine, with ability to infect comandra; (2) urediniospores on comandra, with ability to reinfect comandra plants; (3) teliospores in telia on comandra, which form basidiospores; and (4) basidiospores which may infect pines.

AECIOSPORES

Annual crops of aeciospores are produced in aecia from perennial mycelium in live bark of cankers of pines. At maturity, aecial peridia rupture and expose dark-orange masses of many thousands of teardrop-shaped aeciospores. These spores are disseminated by wind and function as the primary inoculum for infection of comandra.

Effects of Temperature on Germination

Method.–Aeciospores collected in June from recently ruptured aecia were tested for their ability to germinate at several temperatures. Six samples representing Cache, Targhee, Teton, and Wasatch National Forests were tested. Spores were collected with a small cyclone separator, stored in gelatin capsules, and kept cool until tested within a few days. Collodion membranes floating on distilled water in petri plates were used as the substrate for germination. These membranes were made by pressing large drops of collodion between two glass slides, separating the slides, air-drying the exposed surfaces, and finally floating the membranes off onto water. Such membranes were uniformly a few microns thick and proved excellent for aeciospore germination. Small masses of spores were blown through a cyclone separator into a 40-cm.-high settling tower where spores fell onto the test membranes. Germination was simultaneously tested at 5° C. intervals from 3° to 33° C.±0.5° C. After spores had been incubated 24 hours in darkness, a sodium hypochlorite solution (1 percent available Cl) was atomized onto test surfaces to inhibit further germination. Percent germination was determined by counting at least 200 spores, and length was measured in 20 germ tubes. Counts and lengths were taken using a microscope; fields of view were not chosen systematically, but instead the observer attempted to scatter views over the test surface by moving the slide more or less at random. Evaluations of germination of other spore stages presented in this paper were made by this technique unless otherwise indicated.

Results.–Although germinating aeciospores frequently formed several germ tubes, one tube usually became dominant (fig. 3). When both percent germination and length of dominant germ tubes are considered, temperatures between about 8° and 18° C. are most favorable for vigorous germination, but good germination occurs over a broader range (fig. 4). Only at the extremes of 3° and 28° to 33° C. was germination poor.

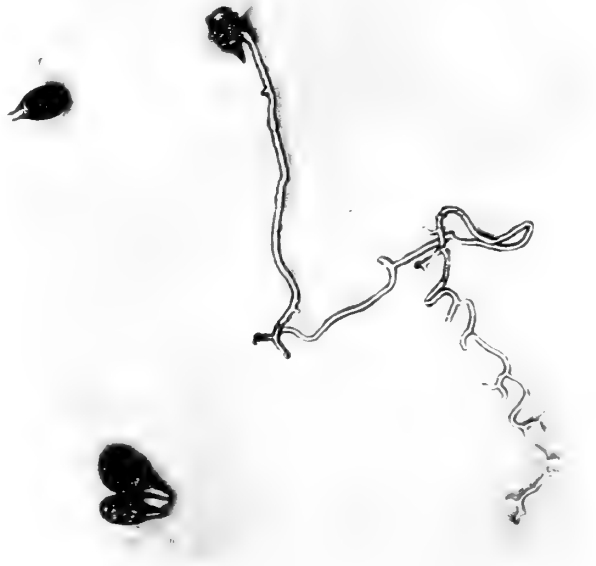

Figure 3.–Germination of *C. comandrae* aeciospore after 24 hours, incubation (X 200). Note the distinctive teardrop shape of nearby aeciospores.

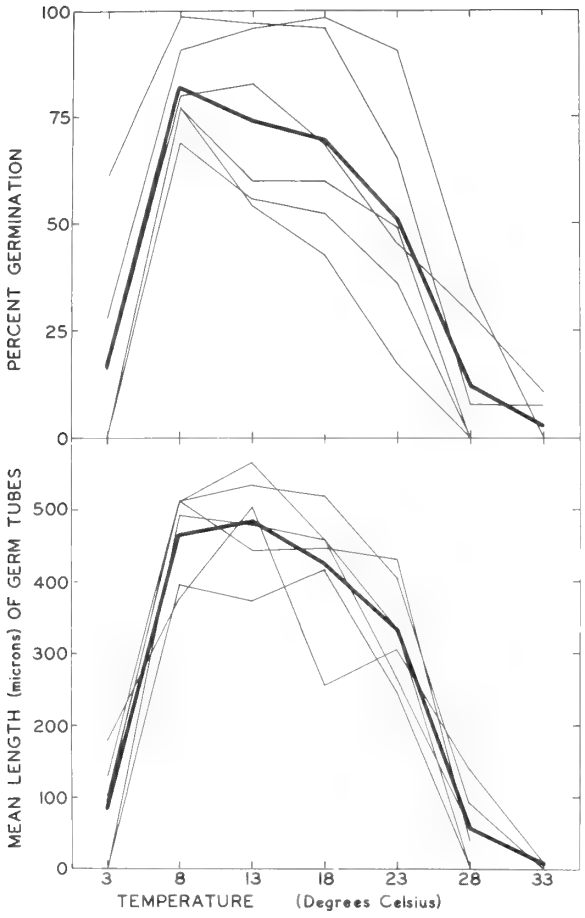

Figure 4.–Germination of aeciospores after 24 hours' incubation at several temperatures. The darker lines are means of the individual samples.

An exploratory test also was conducted to determine how quickly aeciospores germinate and germ tubes grow. Methods used to collect and prepare spores were similar to those described above, but only one collection (Cache National Forest) was tested. Germination of spore groups was stopped after incubation periods varying from 3 to 48 hours. Results indicate that most viable spores germinate within the first 3 hours of incubation at favorable temperatures and that germ tubes continue to grow for more than 24 hours (table 1).

Effects of Light on Germination

The tests of temperature effects were run in darkened chambers and probably indicate what would happen at night in field conditions. In other tests, aeciospores germinated equally well in low light such as might be present on cloudy days. Germination was nil in tests in direct sunlight, but in the field there would rarely be sufficient moisture for germination while there was bright sunshine. Apparently contact with free water is necessary, as evidenced by failure of spores to germinate when tested on glass surfaces in moist chambers if free water has not contacted spores.

Effect of Exposure on Viability and Infectivity

Tests also were run to determine how well the disseminated spores could withstand the kind of waiting period that may pass in the field before moisture and temperatures become favorable for germination. Fresh aeciospores were deposited on shoots of live comandra plants in a glasshouse where temperatures between 10° and 21° C. were maintained. Surface temperatures[2] of comandra leaves remained within a few degrees of air temperatures. At intervals, leaves were plucked from shoots, pressed lightly against 2 percent water agar, and removed. Aeciospores were thereby transferred to the stickier agar surface. Examination showed that aeciospores had not germinated during their exposure on leaves.

Aeciospores on water agar were then placed in moist chambers, and incubated at 18° C. for 24 hours. Examination proved that some aeciospores had remained viable more than 20 days (table 2) at these rather mild conditions.

Infectivity of aeciospores was tested after the spores were exposed to field conditions in Cache National Forest at about 6,000 feet elevation. During 1966, aeciospores were deposited on comandra shoots at various times in an area where natural infection occurs only in unusual years. (None was detected during these tests.) The ability of aeciospores to remain infective was estimated from the degree of development of uredinia on test plants after a period of mild, moist weather that would allow infection. A hygrothermograph in a shelter described by Hungerford (1957) and a recording rain gage within 50 feet of all test shoots provided data on time elapsed between deposition and conditions possible for germination. Uredinia developed on a few leaves of one plant; aeciospores had been deposited 3 days before a trace of rain that made conditions favorable for germination. Other plants on which spores had been deposited 6, 10, and 22 days before conditions

[2] *Measured with thermocouples of overlapped and soldered wires 0.05 mm. in diameter.*

Table 1.–*Influence of time on germination of aeciospores at cool, moderate, and warm temperatures*

Time (hours)	Germination			Mean germ tube length		
	Temperature (degrees C.)			Temperature (degrees C.)		
	8	18	28	8	18	28
	Percent			*Microns*		
3	85	66	0.0	50	140	0
6	78	66	0.0	126	278	0
12	87	70	0.5	363	421	40
24	94	72	1.0	451	495	95
48	91	75	1.0	598	526	70

became favorable for germination displayed no signs of the rust. Comparison of measurements made with thermocouples under similar conditions in Cache National Forest suggests that leaf surfaces had commonly reached 25° to 35° C. at midday. This ability of aeciospores to retain viability for even a few days under severe summer field conditions certainly must enhance spread of *C. comandrae* to comandra.

UREDINIOSPORES

Following infection, annual mycelium develops in leaves and stems of comandra. This soon gives rise to uredinia, which rupture and expose hundreds of yellowish ellipsoidal urediniospores. These spores are disseminated by wind and function as secondary inoculum for additional infection of comandra. This spore stage can quickly intensify the rust in comandra over distances of several miles.

Fresh urediniospores collected in July were tested for their ability to germinate at various temperatures. Tests were run with spore samples from Cache and Wasatch National Forests, and from greenhouse plants that had been inoculated with Cache National Forest spores. The techniques of collecting spores, depositing them on test substrate, and analyzing results were similar to those used in testing aeciospores. However, 2 percent water agar (about pH 6.7) was used exclusively as the test substrate for urediniospores.

Germination of urediniospores was commonly by multiple germ tubes, one of which usually became dominant (fig. 5), but single germ tubes were frequent. Most viable urediniospores produced recognizable germ tubes within the first 3 hours at favorable conditions, and germ tubes grew for more than

Table 2.--*Viability of aeciospores after exposure on comandra shoots in a glasshouse*

Exposure time (days)	Germination[1]	Mean germ tube length[2]
	Percent	*Microns*
0	34	299
5	46	300
11	20	242
21	16	209
28	0	0

[1] *Based on 200 spores.*
[2] *Based on 10 germ tubes.*

24 hours (table 3). On the basis of both percent germination and length of germ tubes at 24 hours, germination seemed best between 13° and 23° C. and poor at 3° C. and at 28° C. or higher (fig. 6). Like aeciospores, urediniospores germinated equally well in low light (such as might occur on cloudy days) and in darkness, but did not germinate in bright sunlight.

Urediniospores were also deposited on comandra shoots in the Cache National Forest plot mentioned earlier. In two trials in which 10 days of conditions unfavorable for infection followed deposition, no shoots became infected. However, uredinia developed on shoots in two trials in which only 6 days of unfavorable conditions followed spore deposition. Thus, even during short dry spells in a warm summer, dissemination of urediniospores can lead to infection of comandra.

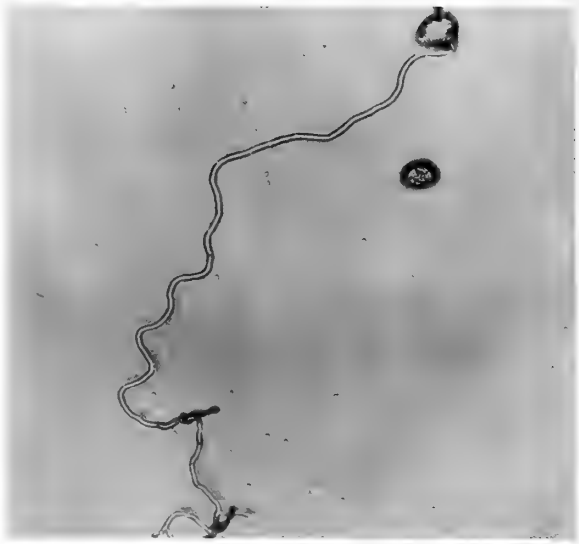

Figure 5.--Germinated urediniospore after 24-hour incubation (X ~~437~~ 175).

TELIOSPORES

Telia contain up to several hundred teliospores bound firmly together as hairlike projections on comandra leaves (fig. 7) and stems. As soon as conditions are favorable, each teliospore may germinate in place and form a basidium and (usually) four basidiospores that are disseminated by air (Hedgcock and Long 1915). This process, referred to here as basidiospore casting, may lead to the dispersal of many hundred airborne basidiospores from each telium. Thus telia and teliospores are not themselves disseminated, but produce the wind-disseminated spores that infect pines.

Effects of Humidity on Germination

To determine whether saturated air is necessary for germination of teliospores, telia were tested in petri-plate chambers in which humidity was controlled by saturated salt solutions or distilled water (table 4). Excised telia from comandra leaves were stuck by their basal ends to petrolatum on the inside of petri-plate covers, and glass slides were placed beneath the telia to catch dispersed basidiospores. Plates were sealed and incubated in darkness at 20° ± 0.1° C. for 24 hours. Slides were then examined microscopically for the presence of basidiospores. They were found on slides in chambers in which relative humidity was 100 percent, but not on slides in chambers in which humidity was 98 percent or lower (table 4).

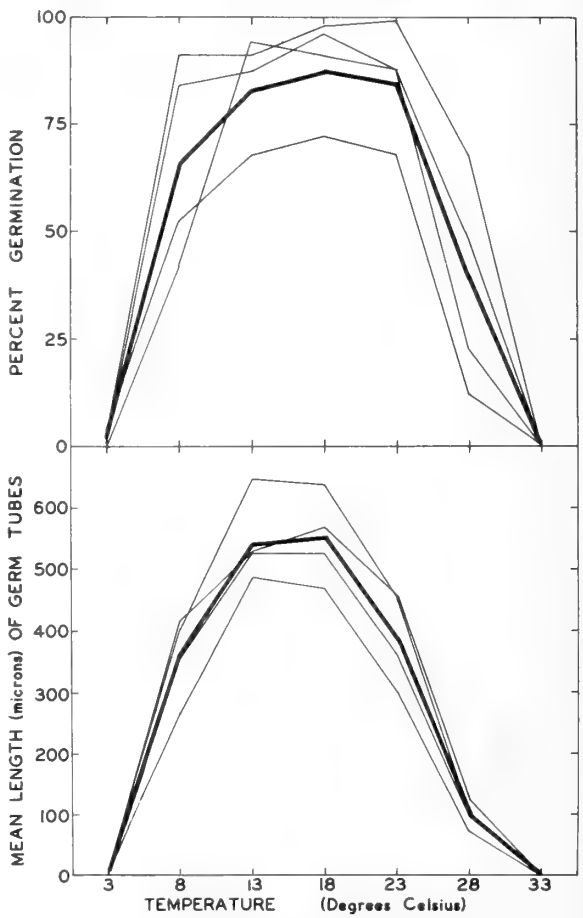

Figure 6.–Germination of urediniospores at several temperatures after 24-hour incubation. The darker lines represent means of four individual trials.

Table 3.–*Influence of time on germination of urediniospores at cool, moderate, and warm temperatures*

Time (hours)	Germination			Mean germ tube length		
	Temperature (degrees C.)			Temperature (degrees C.)		
	8	18	28	8	18	28
	Percent			*Microns*		
3	86	96	67	53	157	64
6	95	94	87	135	270	84
12	93	96	76	311	376	109
24	99	98	83	420	520	116
48	96	99	88	450	541	124

Effects of Temperature on Germination

Method.--Fresh telia from inoculated comandra in a greenhouse were placed in petri-plate moist chambers maintained at various temperatures, to an accuracy of about ±0.5° C. Excised telia were attached vertically by their bases on 2 percent water agar on the insides of plate covers. When teliospores germinated, basidiospores fell onto plates containing 2 percent water agar (adjusted with HC1 to pH approximately 2.0 to prevent germination of the basidiospores, which makes counting difficult). After 3, 6, 12, 24, 48, and 72 hours, the covers were rotated by hand so that time of spore casting could also be determined. Teliospore germination was evaluated by counting the basidiospores cast from whole telia.

Results.–Excellent casts of basidiospores were produced at temperatures of 13° to 23° C.; casts were fair but slower at 8° C., and poor at 6° and 24° C. (fig. 8). No basidiospores were cast at 3° or 25.5° C. and higher. At 25.5° C., basidia formed but no basidiospores developed. At 28° and 30.5° C., not even basidia formed. Comparisons by Duncan's New Multiple Range Test (Duncan 1955) at the 0.01 level indicated that the excellent casts at temperatures 13° to 23° C. were not significantly different from each other at 12 and 24 hours, but were better than casts at other temperatures and continued to be greater throughout the remainder of the 72-hour incubation period. In other similar tests the relative position of the maximum casts varied between 13° and 22° C., but at 25° C. and higher there were never any casts, and longer incubations were always required at temperatures less than 13° C. These results are a refinement over an early report by Mains (1916). He reported no germination at 10° and 30° C., fair germination at 18° C., and good germination at 24° C.

Figure 7.–Telia of *C. comandrae* on comandra leaves (X 9). Telia are common on both upper and lower surfaces of leaves and on stems of *Comandra umbellata* ssp. *pallida.*

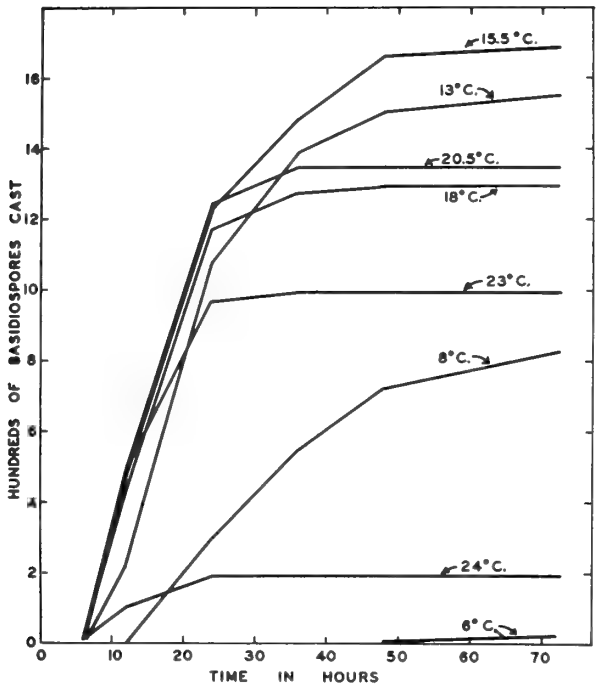

Figure 8.–Germination response of teliospores to several temperatures. Each curve represents the cumulative mean from 10 telia.

Figure 9.–Clock-drive unit that automatically rotates cover of large petri plate. When telia are attached to the cover, basidiospores are cast onto the stationary bottom of the petri plate so as to reveal by their position when casting occurred.

Effects of Freezing and Heating on Viability

The effect of freezing temperatures on viability of teliospores was tested under laboratory conditions. Fresh telia produced from greenhouse inoculations were excised from comandra leaves. These telia were then subjected to below-freezing temperatures such as occur during mild to severe frosts in the field (table 5). Each treatment was replicated with nine telia of equal size for each temperature. After exposure, telia were incubated at 18° C. for 72 hours in moist chambers and basidiospores cast were counted.

As shown in table 5, freezing reduces the ability of telia to cast basidiospores. This effect occurred whether or not the process of germination had already begun at the time of freezing; basidiospore casts were suppressed in telia frozen immediately after removal from comandra leaves and also in telia previously incubated under conditions favorable for germination. Suppression increased with increasing severity of freezing treatment.

Fresh *C. comandrae* telia from Cache National Forest were also subjected to warm temperatures to determine if heat might suppress subsequent casting of basidiospores as it has been shown to do in *C. ribicola* (Van Arsdel et al. 1956). All telia in each trial were of nearly equal size, and no previous germination had occurred. Five telia were used for each treatment. Both dry telia (placed in paper bags) and telia in moist chambers were exposed to heat treatments (table 6). As in earlier tests, telia were then placed in moist chambers at 18° C. for 72 hours and basidiospores cast were counted.

Heat suppressed the ability of teliospores to germinate (table 6) but rather long periods of exposure to warm temperatures were necessary. It would seem unlikely that in pine areas of the Rocky Mountain States warm temperatures would last long enough to alter teliospore germination.

Influence of Light on Germination

To test the influence of light, freshly excised telia from inoculated comandra were stuck to the inside covers of petri plates, as described earlier for temperature studies, and were placed in natural or artificial light or in darkness. The covers were contin-

Table 4.--*Influence of relative humidity on teliospore germination at 20° C. ± 0.1*

Relative humidity (percent)[1]	Saturated salt solution	Mean number basidiospores cast[2]
20	KAc	0
70	KC1 + NaC1	0
90	$ZnS0_4$	0
98	$K_2 Cr_2 0_7$	0
100	Water only	960

[1] *Basis for relative humidity values from Winston and Bates (1960) and Riker and Riker (1936).*
[2] *Based on 5 telia per treatment at each relative humidity.*

Table 5.--*Effects of freezing on teliospore germination*

Freezing period (hours)	Mean number basidiospores cast[1]			
	Freezing temperature (degrees C.)[2]			
	-1	-4	-8	-12
Not preincubated:				
0 (control)[3]	812	589	594	622
6	778	294**	144**	155**
24	511*	212**	101**	81**
Preincubated:[4]				
6	789	422*	46**	0**
24	167**	331**	73**	0**

[1] *Based on 9 telia per treatment at each temperature.*
[2] *Temperatures ±0.5° C.*
[3] *A control group was set aside to correspond to each series of tests at a particular temperature. Sizes of telia within all treatment groups at a single temperature were similar, whereas sizes varied between temperature series.*
[4] *Placed in moist chamber for 6 hours at 18°C.*
andSignificantly less than control at the 0.05 and the 0.01 levels, respectively, as detected by Duncan's New Multiple Range Test (Duncan 1955). Comparisons were made between treatments within each temperature series.*

uously revolved by a clock-drive mechanism (fig. 9) and germination was analyzed according to the numbers of basidiospores that fell onto 2 percent water agar (pH 2) in the plates. In the counting process, the casts were divided into intervals corresponding to 3 hours of cover revolution. These tests were run in a plant growth chamber with 'cool white' fluorescent lights supplemented by incandescents and in a glasshouse on several overcast days. Germination was tested under varying light conditions. Light inside petri plates was about 1,000 foot-candles in the growth chamber and up to 800 foot-candles in the glasshouse (fig. 10). Care was taken during incubation to balance temperatures within dark and lighted plates. (Temperatures were measured with thermistors inside the plates and the plates were moved to warmer or cooler levels of the growth chamber as needed.) Higher levels of light were not included, as it proved impossible with this technique to keep temperatures within limits necessary for germination when more light was supplied.

From the excellent casts of basidiospores indicated in the graph for both light and dark conditions, it appears likely that teliospores could germinate in the field during nights and during overcast days if temperature and humidity requirements are met.

BASIDIOSPORES

Basidiospores of rust fungi require a suitable environment during dissemination to maintain viability. Basidiospores of other conifer rusts have been shown to be adversely influenced by high temperatures, low humidity, and sunlight (MacLachlan 1935, Hirt 1935, and Spaulding and Rathbun-Gravatt 1926). The influence of these factors was studied in *C. comandrae* basidiospores.

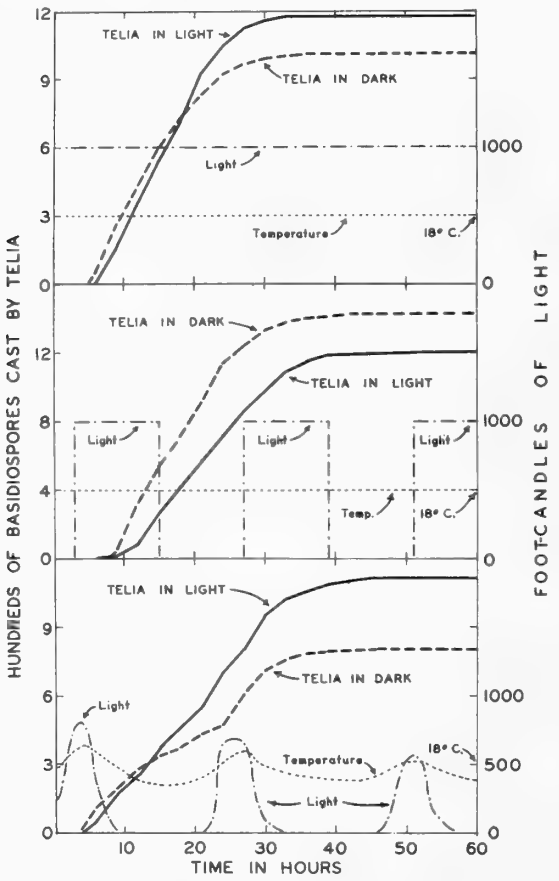

Figure 10.–Germination of teliospores, based on cumulative numbers of basidiospores cast from telia in light and darkness. The upper two graphs represent trials run in the growth chamber. In the first, the "light" group of telia was exposed constantly at the 1,000-foot-candle level. In the second, the "light" group was exposed at regular intervals as shown. The lowest graph represents the trial run in a glasshouse, where the "light" group was exposed to natural intervals of light and darkness. Temperatures were held constant in the growth chamber and fluctuated somewhat in the glasshouse, as shown by the dotted lines.

Freshly formed basidiospores were collected on glass slides and on 2 percent water agar. For collection, glass and agar were exposed for 1 hour beneath germinating telia in moist chambers at 15° to 22° C. The basidiospores were immediately exposed outdoors. During exposure, surface temperatures of the glass and agar were measured with thermocouples. After exposure, the basidiospores were incubated on 2 percent water agar at 18° C. for 24 hours. Viability was then measured by percent germination.

Basidiospores were sensitive to exposure, but survived sunlight well for at least 2 hours when kept in contact with a moist substrate (table 7). Viability declined more quickly in basidiospores exposed directly on glass, even when the slides were shaded by lodgepole pine.

The influence of relative humidity on retention of viability of basidiospores was studied. Basidiospores were obtained by exposing glass slides beneath telia germinating at 18° C. in dark moist chambers. After 1 hour of deposition, the slides were transferred inside a mist chamber to dark chambers in which relative humidity was controlled by glycerol solutions as described by Scharpf (1964). Following exposures of ½, 2, 4, and 20 hours at controlled humidities, basidiospores were transferred inside a mist chamber to 2 percent water agar, and were incubated 24 hours at 18° C. Spore viability was evaluated by percent germination based on at least 200 spores.

Relative humidity had a pronounced effect on survival of basidiospores. Survival diminished with increasing exposure time in less-than-saturated atmosphere (fig. 11) and decreased most rapidly at lower humidities. It was only slightly better at 10° than at 20° C. Thus it would seem that only basidiospores disseminated during damp weather would be viable.

The influence of temperature on germination of freshly cast basidiospores was studied. Spores were incubated in unlighted chambers in which temperatures were controlled to an accuracy of ±0.5° C. After incubation (24 hours except in time tests), further germination was inhibited by application of 1 percent chlorine. Percent germination, based on at least 200 spores, and mean length of 20 germ tubes were then determined.

The percentage of spores that germinated increased for more than 24 hours at 8° and 28° C., but reached its maximum in 6 hours at 18° C. (table

Table 6.–*Effect of high temperatures on subsequent teliospore germination*[1]

Exposure time (hours)	Mean number basidiospores cast[2]				
	Temperatures (degrees C.)[3]				
		26		30	
	Control	Dry	Moist	Dry	Moist
0	850				
4		890	860	567	600
8		674	710	910	655
24		702	372**	396**	149**
48		240**	68**	266**	154**
72		170**	11**	262**	33**

[1] *Based on whole telia prepared as described in text.*
[2] *Based on 5 telia for each treatment.*
[3] *Temperatures ±0.5° C.*
** *Significantly different from control at 0.01 level as detected by Duncan's New Multiple Range Test (Duncan 1955).*

Table 7.–*Effect of exposure to outdoor conditions on viability of basidiospores*

Exposure treatment	Subsequent germination
	Percent[1]
Midday December sunshine in Logan, Utah, at -1° to -6° C. air temperature:	
½ hr. on dry glass	0
½ hr. on water agar	99
2 hr. in distilled water	88
Midday August sunshine (6,000 to 7,000 foot-candles) on Cache NF near Beaver Mountain:	
½ hr. on glass at 24% r.h. and 22° to 29° C.	91
1 hr. on glass at 19% r.h. and 34° to 41° C.	0
½ hr. on water agar at 17° to 22° C.	100
1 hr. on water agar at 17° to 22° C.	100
2 hr. on water agar at 19° to 23° C.	85
Midday August shade (200 foot-candles) near Beaver Mountain:	
1 hr. on glass at 28% r.h. at 25° to 30° C.	29

[1] *Based on a sample size of from 47 to 200 spores.*

8). Germination was usually by a single germ tube that continued growing for more than 24 hours. Excellent germination and germ tube development occurred from about 8°-13° to 23°-28° C., but germination was poor at the extremes of 3° and 33° C. (fig. 12).

In other tests, telia that had been in storage at 5° to 7° C. for several weeks often produced basidiospores, many of which germinated by forming either secondary basidiospores or short (<10μ) broad germ tubes, rather than by forming normal tubes, which generally reach more than 100μ in 24 hours. Such abnormal types of germination are also seen occasionally in basidiospores cast from field collections of older telia, but not in those cast from fresh young telia.

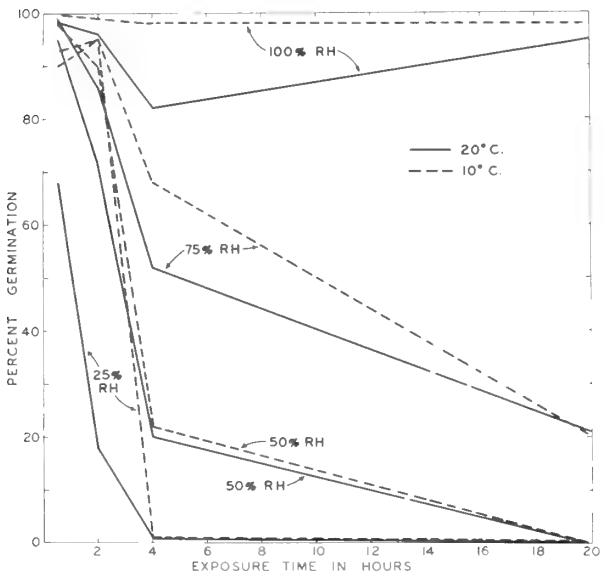

Figure 11.–Survival of basidiospores after exposure to various temperatures and relative humidities, as indicated by subsequent basidiospore germination.

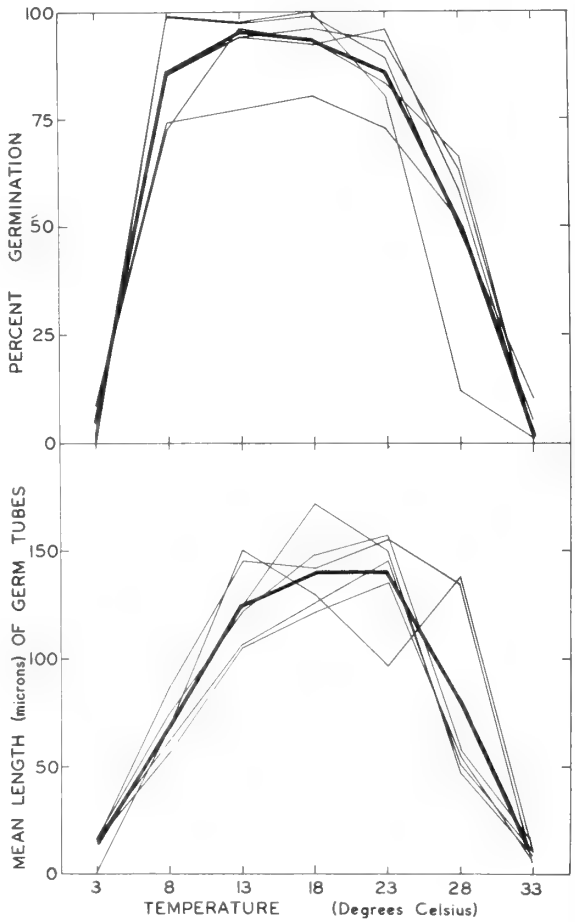

Figure 12.–Germination of basidiospores at several temperatures after 24 hours' incubation. The darker lines are mean curves of the individual trials.

Table 8.–*Influence of incubation time on germination of basidiospores at cool, moderate, and warm temperatures*

Time (hours)	Germination			Mean germ tube length		
	Temperature (degrees C.)			Temperature (degrees C.)		
	8	18	28	8	18	28
	Percent			*Microns*		
3	0	28	6	0	16	8
6	0	100	17	0	26	13
12	64	100	35	18	85	21
24	94	100	54	76	159	29
48	85	100	65	130	243	38

INFECTION

Comandra, jack pine, ponderosa pine, and lodgepole pine have previously been infected with comandra rust in experimental trials (Adams 1919, Anderson 1960, Andrews et al. 1963, and Hedgcock and Long 1915). However, virtually nothing is reported about the processes of infection or the influence of moisture, temperature, or host phenology on infection. Some information on these factors was obtained in the following trials.

COMANDRA

Penetration of comandra was observed with an incident light microscope and with a normal light microscope when leaves were cleared by the lactophenol-chloral hydrate technique (Riker and Riker 1936) and stained with aniline blue. Both aeciospores and urediniospores germinated well on leaf surfaces. Appressoria formed when germ tubes contacted stomates (fig. 13), and infection pegs could be seen penetrating between the guard cells of stomates. This was the only type of penetration seen in comandra.

The influence of temperature during inoculation of comandra was studied under controlled conditions. Comandra that had been growing in flats in Logan for at least a year were used as test plants. At the time of inoculation, shoots were about 2 months old. Inoculum consisted of fresh aeciospores and urediniospores originating in Cache National Forest. Approximately equal numbers of spores were deposited on test shoots by the settling tower method described earlier for aeciospore germination tests. The flats were then placed in controlled temperature (±1° C.) chambers in darkness. Distilled water was atomized intermittently in the chambers and small water droplets remained on leaves throughout the inoculation. After specified times in the mist chambers, the flats were moved to shaded portions of a well-ventilated greenhouse until moisture on the shoots dried (5 to 20 minutes). The flats were then placed on greenhouse benches and shoots were examined periodically for the presence of uredinia. A few days after the emergence of the first uredinia, the numbers of infection spots (evidenced by yellow color, swelling, and uredinia) on test shoots were counted.

Infection of comandra occurred over a wide range of temperatures with both aeciospore and urediniospore inoculum (table 9). Although infection spots increased with longer mist periods, 12 to 24 hours was sufficient for abundant infection at moderate temperatures. In followup trials, infection occurred in as little as 5 hours in a mist chamber at about 20° C.

In other experimental inoculations, it was easy to infect comandra shoots in a juvenile stage (1 week after emergence, when the purple shoots were only a few centimeters tall), through maturity, and until normal leaf abscission. Thus it appears that comandra is highly susceptible at any stage of development during the growing season.

At greenhouse conditions of about 13° to 24° C., 10 to 15 days generally passed from the

Figure 13.–Appressorium, at end of aeciospore germ tube, attached to stomate of a comandra leaf (X 850).

Table 9.–*Influence of temperature and time on infection of comandra in mist-chamber inoculation tests*

Inoculum and time in mist chamber (hours)	Mean number infections per leaf						
	Temperature (degrees C.)						
	3	8	13	18	23	28	33
Aeciospores:							
0 (Control)[1]	0	0	0	0	0	0	0
12	0	5	0.2	6	8	Shoots died[2]	
24	0.1	7	7	9	8		
48	0	8	8	26	8		
72	0	9	9	25	8		
Urediniospores:							
0 (Control)[1]	0	0	0	0	0	0	0
12	1	4	6	9	7	Shoots died[2]	
24	2	8	7	9	10		
48	3	8	11	10	10		
72	5	7	11	11	10		

[1] *A corresponding control group was set aside for each temperature series for each type of spore.*
[2] *Apparently killed by environmental factors associated with the warm mist treatment and subsequent drying.*

beginning of an inoculation until uredinia emerged through leaf surfaces, although the uredinia were sometimes visible beneath the epidermis after only 6 or 7 days. Telia generally emerged 20 to 30 days after inoculation, but in one instance they developed after only 10 days had elapsed. Sometimes, especially late in the growing season, the uredinial stage is bypassed and only telia form. Artificial inoculations we made in Cache National Forest in spring generally resulted in uredinia in 2 to 3 weeks and telia in 4 to 6 weeks.

PINE

All reported experimental infection of pines has been with telial inoculum that had presumably passed through the basidiospore stage before the infection. Meinecke's (1929) attempts to inoculate pines with aeciospores by his wounding and spore-showering techniques, which were successful with *Peridermium harknessii,* were unsuccessful with *C. comandrae,* as might have been anticipated with this heteroecious rust fungus.

The possibility of mycelial transfer by rodents and insects has also been investigated. More than 100 attempts in the field to transfer the rust by bark inserts and bark patch grafts (means used successfully by Hedgcock and Hunt 1920 and Patton 1962 with other conifer stem rusts) have failed for *C. comandrae.* This might indicate that the odds are against successful mycelial transfer by insects or rodents, particularly under natural conditions that would probably be harsher than those in the trials. Therefore it seems reasonable that pine infection in the field results only from infection by basidiospores.

My attempts to detect penetration by means of tissue clearing and incident-light microscopy have failed, so the process of infection remains a mystery. However, successful inoculations of seedlings give clues to the influence of temperature and moisture on infection and to the tissues that are susceptible.

Method.–Lodgepole pines midway through their third growing season were inoculated in a mist chamber within a growth chamber. Temperatures were controlled within the mist chamber ±1° C. and the chamber was dark except in one experiment using a programmed temperature cycle.[3] Inoculum from Cache National Forest consisted of fresh comandra shoots with viable telia, placed over the test pines.

[3] *Seedlings were exposed to a cycle of 12 hours of darkness at 5° C., followed by 12 hours of light (about 1,000 foot-candles) at 15° C. The test began with 3 hours of light.*

After remaining in the inoculation chamber for 1, 2, and 3 days, the pines were placed in a greenhouse until autumn and then moved to outdoor cold frames.

Results.--Seedlings were examined frequently over a period of 2 years. No infections developed on 50 pines reserved as controls. On inoculated seedlings, no positive indication of infection was noted until the summer following inoculation. Then, infections could be identified only by stem swellings and pycnial droplets that exuded in August and September. Aecia formed and cast aeciospores in May of the next year (fig. 14). The most abundant infection resulted from inoculations at temperatures of 15° and 20° C.; 24 hours in the mist chamber was apparently sufficient for the formation and dispersal of basidiospores, and their germination and infection of pine tissues (table 10). Infection also occurred under less favorable conditions but no infection occurred at 5° or 25° C. From the position of the infections, it was determined that 13 had entered through current year shoots, 11 had entered 1-year-old tissue (three of these might have entered through current year adventitious shoots), and none had entered 2-year-old tissue.

Although no outward signs of the rust were evident in needles, microscopic examination of sections showed rust hyphae in needles attached to stem swellings. Unfortunately it could not be determined if the rust had entered the needles first or had grown out into them from infected bark. However, needles would seem a likely place for infection since direct stem infection by basidiospores of conifer rust fungi has been reported only in primary tissue of current year stems. In the pines tested here, stem elongation had terminated at least a month before inoculation, and periderm tissue had formed.

Figure 14.–Lodgepole pine 21 months after experimental infection with telia of *Cronartium comandrae* from Cache National Forest. Ruptured aecia are present on the upper portion of the swollen stem.

Table 10.–*Influence of time and temperature on experimental infection of lodgepole pine*

Time in mist chamber (hours)	Ratio of infected pines to total pines					
	Temperature of mist chamber (degrees C.)					
	5	10	15	20	25	5-15[1]
24	0/8	0/9	3/11	1/8	0/8	1/8
48	0/8	0/10	3/12	5/8	0/8	1/8
72	0/8	1/10	3/12	1/6	0/8	4/12

[1] *Approximation of natural conditions as described in text, footnote 3.*

OVERWINTERING

Like the other Cronartium rusts of pines, *C. comandrae* overwinters as mycelium in live bark of its pine hosts, and aeciospores may be produced from the same canker for many successive years (Arthur 1929 and Hedgcock and Long 1915). Being an obligate parasite, *C. comandrae* dies along with its host, but the two commonly survive together for a few years or even a few decades. In some unusual instances the mycelium of a single canker may remain active for more than a century (Krebill 1965). Aecial production in long-lived infections often is limited and may not occur in many years, especially when mycelium is in bark that is not very active physiologically. In the form of its long-lived mycelium, *C. comandrae* can exist for long periods in pine stands even when there is no new infection.

C. comandrae is unable to overwinter in comandra in mountain areas near susceptible pines. Infections on stems of comandra are common, but microscopic examination indicates that the rust fungus does not grow down the stems into rhizomes. Thus when the shoots die in the fall, the comandra plant is freed from the rust. Indeed, transplants of severely infected comandra collected in fall from Cache and Teton National Forests sprouted free of rust in Logan the following spring. Likewise, experimentally infected comandra have always sprouted free of rust after overwintering outdoors in Logan.

Although there is no field evidence to suggest that *C. comandrae* can overwinter in the mountains, it may possibly overwinter free from pines in the Great Plains of eastern Colorado (Bethel[4]). The mode of such overwintering is unknown and the observations reported could even be misinterpretation of long-distance dissemination of aeciospores or urediniospores.

[4] *Bethel, E. Some early collections of west American fungi. Unpublished manuscript, filed in Intermountain Forest and Range Exp. Sta., Logan, Utah. 1925.*

PHENOLOGY OF LODGEPOLE PINE, COMANDRA, AND *CRONARTIUM COMANDRAE* IN THE ROCKY MOUNTAIN STATES

Development of comandra blister rust and the corresponding development of comandra and lodgepole pine were studied from 1962 to 1966 in the western part of the Rocky Mountain States. Several plots for which general phenology data were recorded are listed below. The plots are named for the National Forests in which they are located.

Teton–Wyoming, near Goosewing Guard Station in the Gros Ventre River drainage south of Kelly at 7,250 feet with a southern aspect.

Targhee–Idaho, near Pine Creek north of Swan Valley at 5,850 feet with a southern aspect.

Bridger–Wyoming, near Fremont Lake east of Pinedale at 8,500 feet with a western aspect.

Sawtooth–Idaho, on Cassia Plateau west of Oakley at 7,400 feet on a slight northwest slope.

Wasatch–Utah, near Beaver Creek east of Kamas at 7,500 feet elevation on a slight southwest slope.

Each plot consisted of lodgepole pines with 10 marked cankers and 10 marked branch shoots on the same trees, and 10 comandra shoots in nearby open areas. Length of marked shoots and occurrence of spore-producing structures were recorded at least once each month of the growing season.

Analysis of these plots (fig. 15) tells us much about the phenology of the hosts and parasite in the Rocky Mountains. Comandra sprouts early in the spring; it emerges through the soil soon after snowmelt in mid-May or late May. Shoot growth is rapid through June and into early July. Foraging by rabbits and ungulates reduces shoot height, and in autumn after severe frosts, leaves dehisce and stems die. Branch shoots of lodgepole pine begin growing in early June and continue elongating through July. Aecia of *C. comandrae* emerge about the same time that lodgepole pine shoots begin growth and the aecia remain abundant through early summer. Some aecia continue dispersing spores well into autumn and, rarely, new aecia form in early autumn. Pycnia exude after the onset of aecia from late June through August, some continuing into September. Uredinia appear in July about the time comandra shoots attain full height growth and the pines are dispersing pollen. By early autumn, uredinia are inactive. Telia usually appear a couple of weeks after the appearance of uredinia and become plentiful in August. They remain abundant until leaves and stems die in autumn.

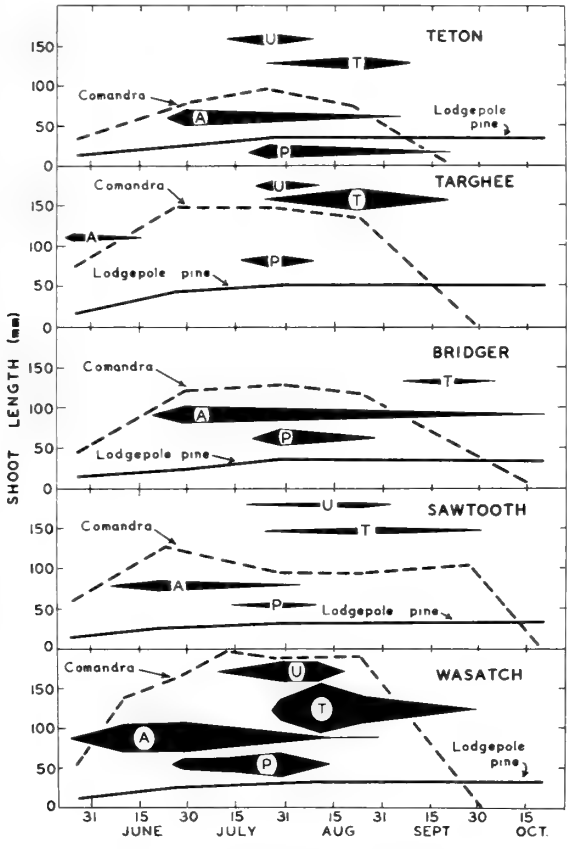

Figure 15.–Phenology of *C. comandrae* and its hosts in several National Forests in 1965. The solid bars represent sporulation in the various stages: A, aecial; U, uredinial; P, pycnial; and T, telial. The vertical extent of the bar indicates frequency of sporulation in relative terms; the horizontal extent of the bar indicates duration on the time scale. The dashed line shows seasonal growth of comandra with reference to the scale of shoot length at left. Growth of lodgepole pine is similarly shown by the solid line.

Elevation

To test the influence of elevation on rust development, four additional plots were established in the Uinta Mountains near the Upper Provo River. All had southwest aspects and were located at elevational increments of approximately 1,000 feet in the lodgepole pine zone of from about 7,000 feet to over 10,000 feet elevation. Comandra was not found above about 8,500 feet in this vicinity even though the rust occurred in cankers near the upper limit of lodgepole pine.

From the evidence of the plots, elevation has a strong influence on phenology (fig. 16). Development of rust was earliest and the season of development was longest at the lowest elevation; with increasing elevation, development of rust was delayed and the season shortened. Since elevation was not so clearly implicated as a factor in results from the other plots (fig. 15), such conditions as aspect and local weather also must affect phenology.

Local Weather

In order to find out more about annual variation in phenology and the influence of local weather, we established plots in the Bear River Mountains of Cache National Forest. Beaver Mountain plot was located at 7,200 feet elevation on a southern aspect in northern Utah, and Fish Haven plot was established at 6,800 feet elevation on a southeastern

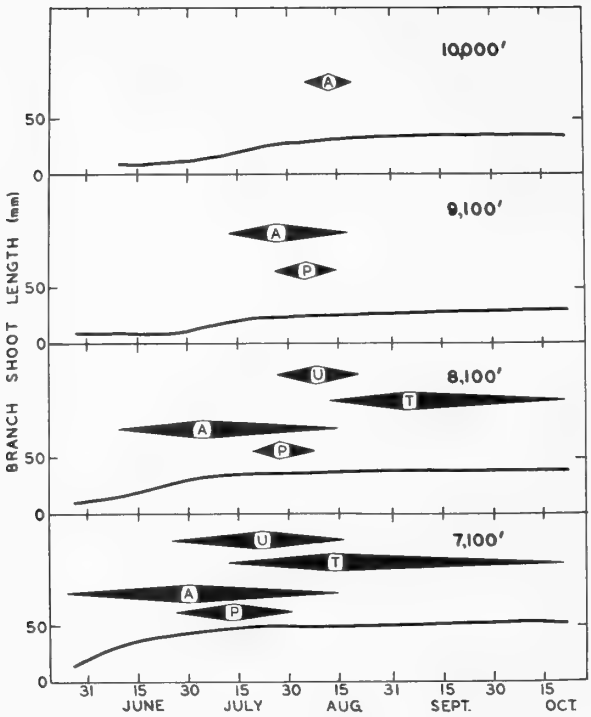

Figure 16.--Phenology of *C. comandrae* and lodgepole pine at four elevations of similar aspect in Wasatch National Forest in 1965. The bars represent presence of spores of various stages: aecial, pycnial, uredinial, and telial. Relative frequency and duration of sporulation are indicated by vertical and horizontal extent of the bar, as in figure 15. Growth of pine in terms of branch shoot length is shown by the curves; comandra was absent at the two higher elevations.

aspect in adjacent Idaho. Temperature and relative humidity were recorded by hygrothermographs in shelters (Hungerford 1957) that were placed so that the sensors were about 4 to 6 feet high near cankers of lodgepole pines and about 0.5 foot to 1 foot high near comandra plants. Precipitation was measured by recording rain gages located in open areas near comandra. Fifteen branch leaders and 30 current-year needles of lodgepole pine, and 15 shoots of comandra were marked and measured weekly. Pollen casting by pine and flowering of comandra were noted. Presence of aecia and pycnial oozing were recorded for 15 cankers in each plot. Development of uredinia and telia on the 15 marked comandra shoots in each plot was also noted. Periods of spore dissemination were determined by spore traps (fig. 17) placed near sporulating structures of infected plants. Seasonal traps consisted of petrolatum- or glycerine-jelly-coated glass microscope slides on a continuously moving belt; an opening above the slides allowed each point on the slides an exposure of 6 hours to deposition of spores by gravity. Trapping was also done intermittently by a suction trap somewhat similar in operation to the Hirst trap (Hirst 1952). Microscopic examination of slides showed the presence of spores, and their position along the slides showed when spores were trapped.

A summary of spore-trapping data, host phenology, and weather is presented in figures 18, 19, and 20. Although aecia were present on some cankers from early June to late September, the vast majority of aeciospores were dispersed in June and July. During June, general rain associated with frontal storms is fairly common in this area. Comandra has already made most of its shoot growth by the time aeciospore inoculum arrives. Perhaps this rust-free period accounts for the ability of comandra to remain

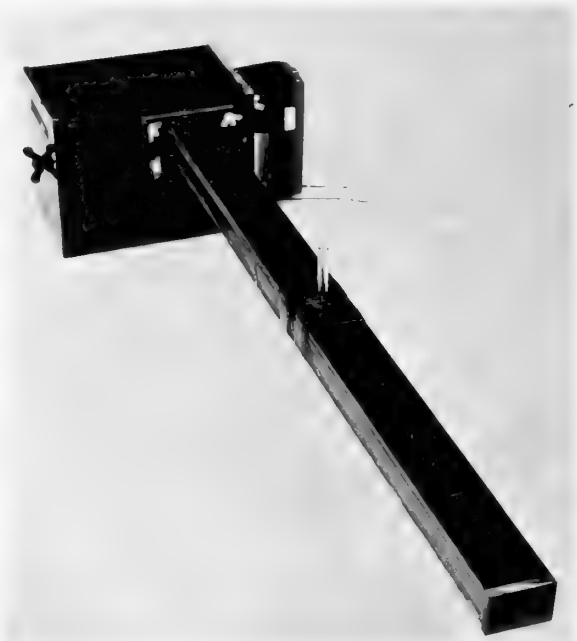

Figure 17.--Spore-trapping device. A clock drive pulls a series of glass slides on a belt beneath an opening. This trap is equipped with a battery-operated exhaust fan so that air is drawn through a glass tube and particles come in contact with glycerine-jelly-coated glass slides. If the intake tube is replaced by a horizontal slit and the exhaust fan is not used, this device can trap particles that settle by gravity onto sticky slides.

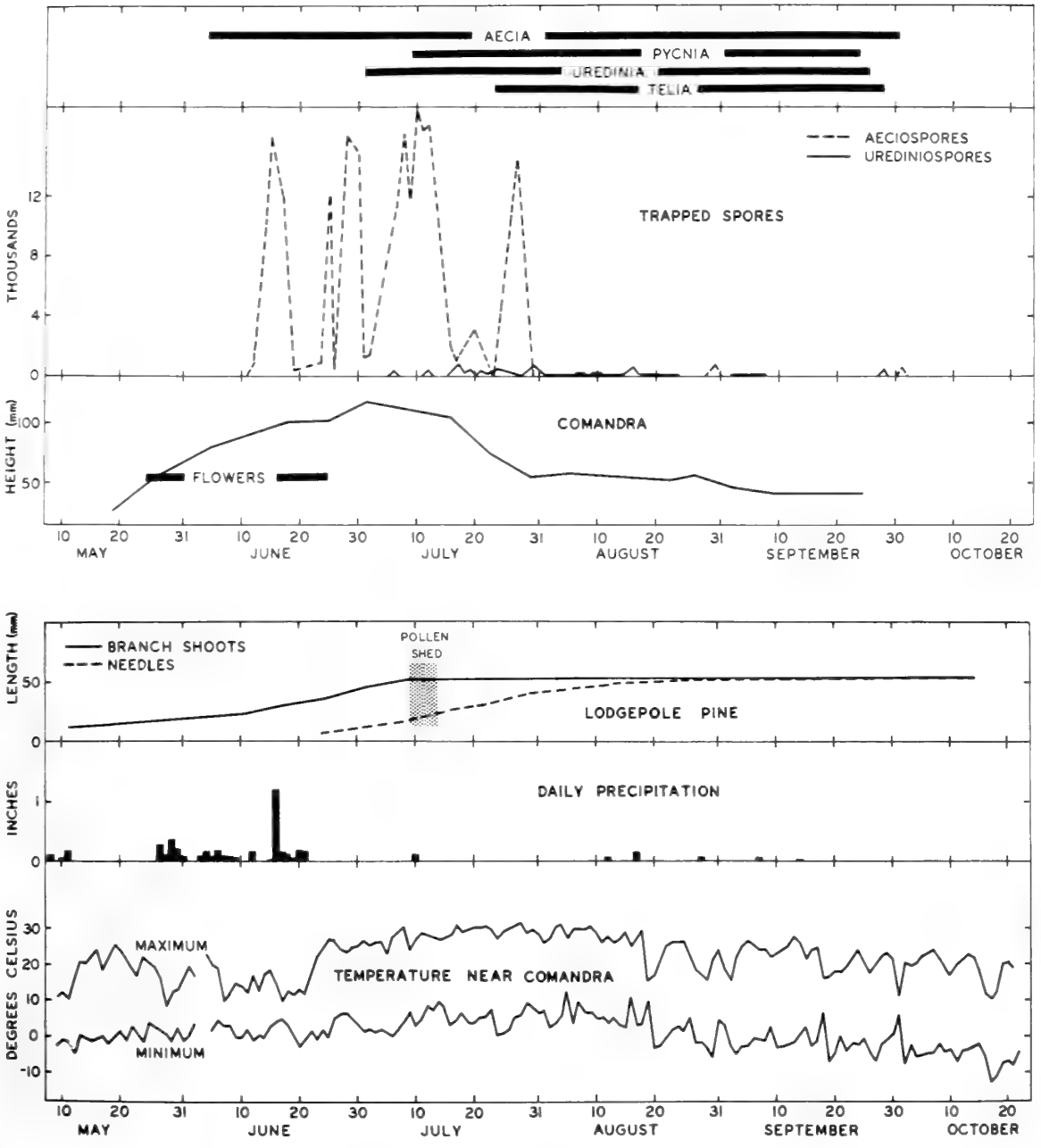

Figure 18.--Phenology of *C. comandrae* and hosts in Beaver Mountain plot in 1964 in response to weather conditions. In these diagrams, the seasonal extent of presence of fruiting bodies, number of spores trapped by gravity, growth of comandra shoots and duration of flowering, and growth of lodgepole pine may be studied in relation to the precipitation and temperature conditions existing during the period May through October.

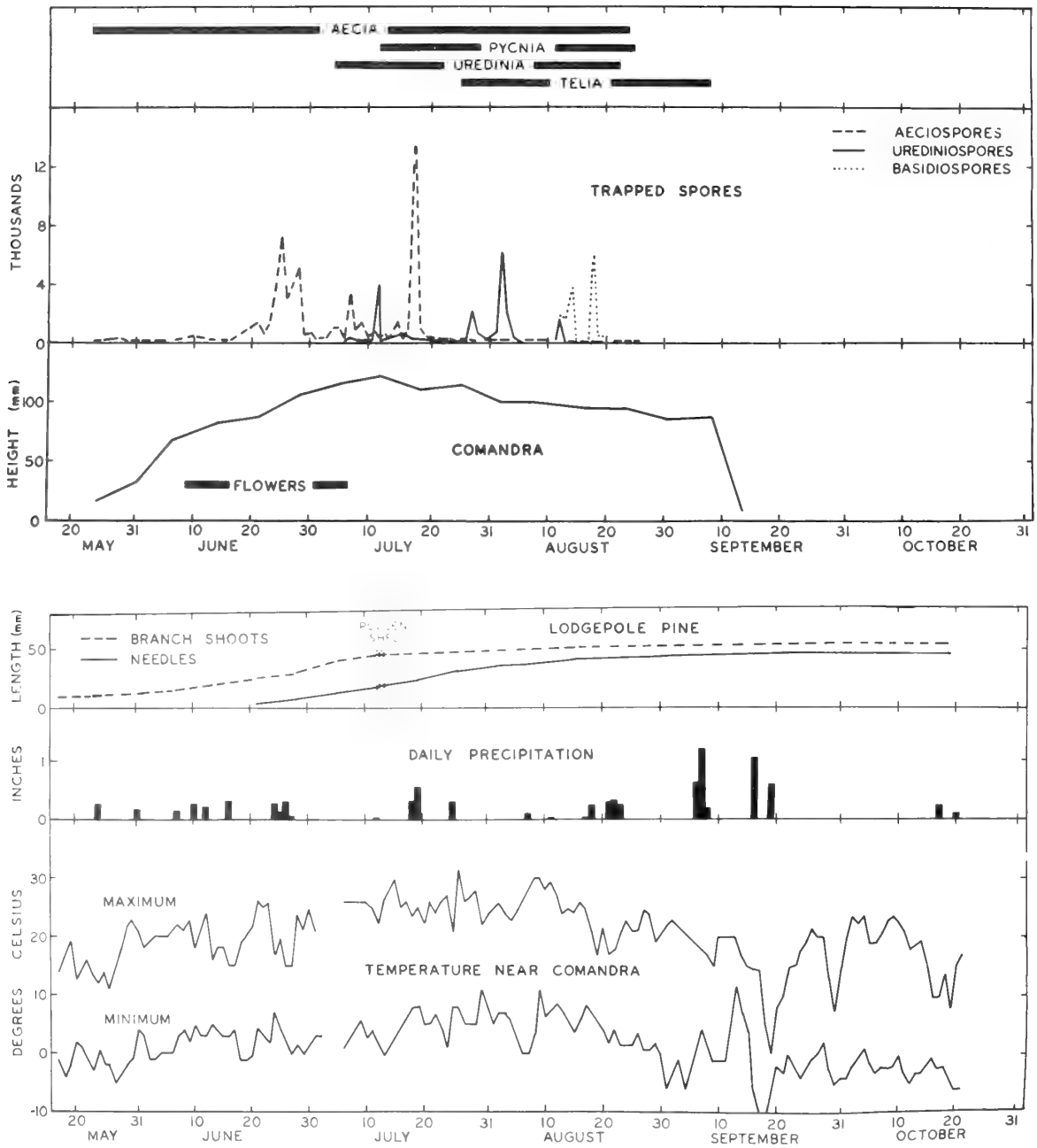

Figure 19.–Phenology of *C. comandrae* and hosts in Beaver Mountain plot in 1965.

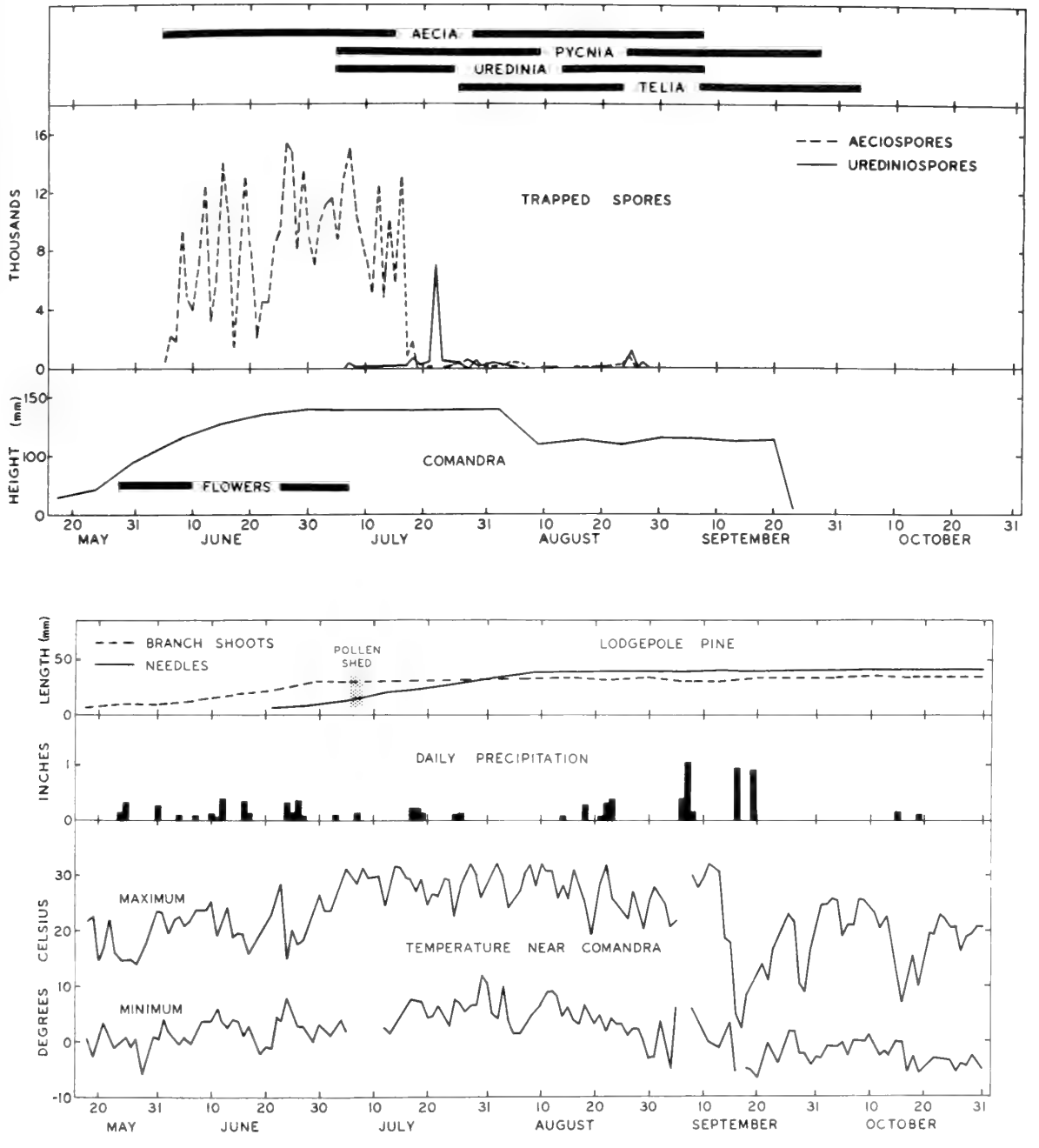

Figure 20.--Phenology of *C. comandrae* and hosts in Fish Haven plot in 1965.

in plant communities near rust-infected lodgepole pine for long periods even though heavily infected by comandra rust almost every year. The combination of susceptible comandra shoots and general rainfall during the period aeciospores are being shed makes conditions suitable for primary infection, as the rust is usually common by mid-July on comandra near infected pine stands. The capability of aeciospores to germinate well at prevailing cool temperatures also enhances primary infection of comandra. By mid-July, aeciospores are reinforced by urediniospores as a source of inoculum. By this time, thundershowers generally prevail and spread becomes more haphazard. Because infection of comandra shoots takes only a short time, thundershowers usually result in some secondary spread. In most years infected comandra can commonly be found a few miles from infected pines, but in 1966, which was drier than normal in July and August, the rust in comandra was rare beyond a few hundred yards from infected pines. Apparently little secondary spread occurred in that year.

Although telia are present from late July until hard frosts in autumn, basidiospores are cast only rarely. Not only were basidiospores rarely trapped, but also visual observations indicated that basidiospore production had seldom occurred. Low temperatures prevent any appreciable cast at night during radiation dew periods even though relative humidity near comandra commonly reaches 100 percent for 4 to 6 hours. Moisture from thundershowers usually does not last long enough to initiate basidiospore casting, but when it does, drying on succeeding sunny days greatly reduces chances of pine infection. By such action the potential of the inoculum may be reduced to the point of limiting infection, even if favorable conditions follow. Therefore, it appears that thundershowers are detrimental to the chances for pine infection.

It seems likely that serious outbreaks of pine infection in the Rocky Mountain States can occur only when large warm storms invade and remain in the area for several days during August or early September when telial inoculum is plentiful and highly viable. As shown in figure 21, heavy rainfall is not necessary for abundant telial germination, but saturated air and long periods of mild temperatures must prevail. Even during those periods when most basidiospores were trapped during these studies (figs. 21 and 22), casting was soon followed by periods of moder-

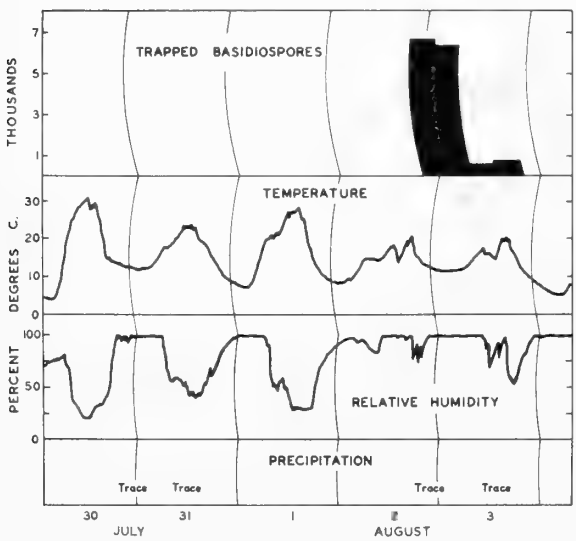

Figure 21.–A successful suction trapping of basidiospores; and the corresponding weather data in Beaver Mountain plot 1966.

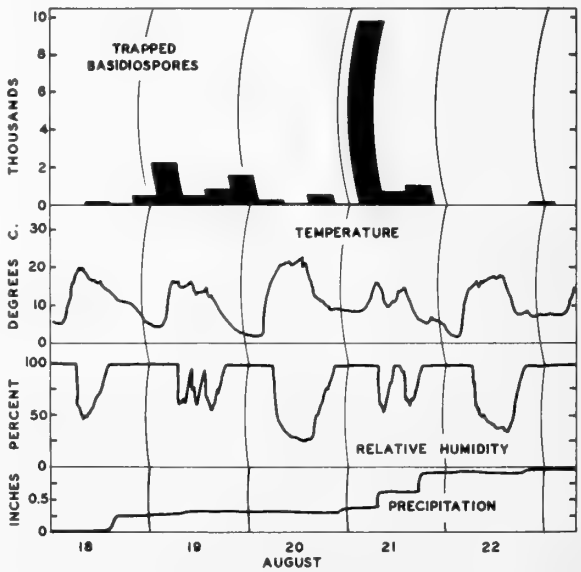

Figure 22.–A successful suction trapping of basidiospores; and the corresponding weather data in Beaver Mountain plot 1965.

ately low relative humidity, and it is doubtful that pine infection could have resulted. In autumn, though longer moist periods associated with frontal storms are again more common, temperatures are probably too cold for basidiospore casting. Thus it seems that weather conditions that could lead to abundant pine infection are rare in the Rocky Mountain States.

Tissue Susceptibility

By the time telia are present on comandra, stems of lodgepole pine have finished elongation and are no longer succulent. This has been taken to indicate that pine infection occurs through needles rather than directly in stems. Whereas results from experimental infection of lodgepole pine and from phenological data indicate that current-year and 1-year-old shoots are probably more susceptible, four young infections found in Teton National Forest in 1966 support a different view. These infections, like those artificially induced, were on needle-bearing stems and had produced about the same degree of swelling; pycnia were exuding apparently for the first time. If we assume that the young trees were infected only 1 or 2 years previously, like the artificially infected seedlings in a similar stage of development, we can conclude that two infections entered 2- or 3-year-old shoots, one a 3- or 4-year-old shoot, and one a 4- or 5-year-old shoot. This apparent contradiction of evidence from my pine infection trials stresses the need for additional information on susceptibility of tissues.

Seasonal Spore Viability

Studies were designed to determine viability of spores collected throughout a growing season. Viability at 18° ±0.5° C. was determined with samples collected from fruiting structures once a week. Aeciospores were tested on collodion films on distilled water and urediniospores and basidiospores on 2 percent water agar; teliospore viability (measured by numbers of basidiospores cast from whole telia) was determined in moist chambers over 2 percent water agar at pH 2. Telia were incubated 72 hours and other spores 24 hours. At least 200 aeciospores or urediniospores were examined in each test for percent germination, and 20 each for length of germ tubes. Percent germination multiplied by mean germ tube length gave an index of germination (trends of both percent and lengths were similar).

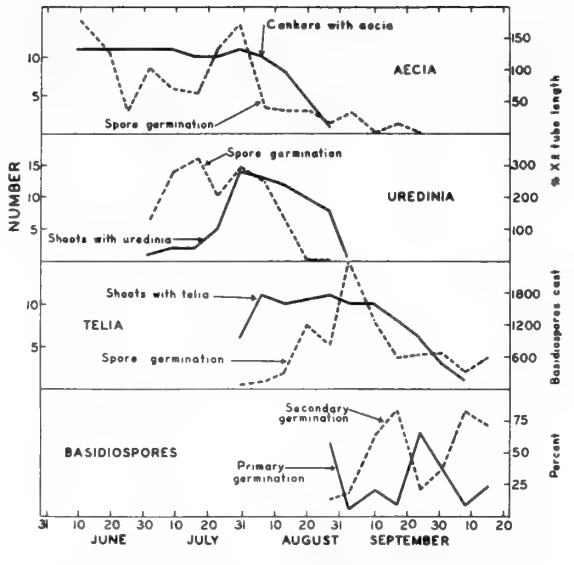

Figure 23.–Prevalence of *C. comandrae* fruiting structures and corresponding viability in Fish Haven plot 1964. In bottom graph, curves are shown for germination by formation of a germ tube (primary) or by production of another basidiospore (secondary).

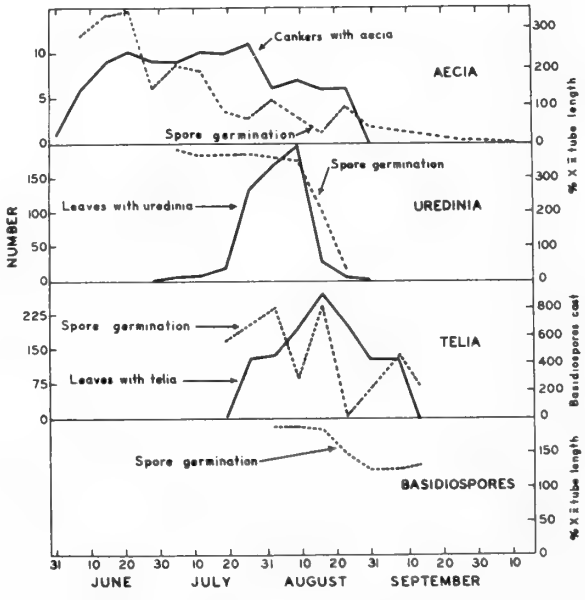

Figure 24.–Prevalence of *C. comandrae* fruiting structures and corresponding viability in Beaver Mountain plot 1965. Since germination of basidiospores during this year was entirely by formation of germ tubes, only one curve is shown.

Viability of aeciospores and urediniospores was highest during June and July and tapered off in mid-August and into September (figs. 23 and 24). Thus the chances of additional comandra infection in late summer and autumn are diminished in two ways–the inoculum is reduced in quantity and the spores are less able to infect comandra because of reduced vigor of germination.

As telia elongate by formation of new teliospores, their ability to cast basidiospores increases, and they become highly viable in early August. Telial viability then decreases irregularly over the rest of the season. Decreases result from occasional germination of teliospores and possibly from aging and daily exposure to near-inhibitory high and low temperatures. New telia and new teliospores continue to form, and the ability of telia to cast basidiospores may again increase somewhat. Viable telia are present until death of the host shoot, even though the number of spores cast is reduced late in the season.

The evidence as to the ability of basidiospores to germinate is more confusing. In general, germination by germ tubes decreased as the season progressed. Sometimes this was because secondary basidiospores were formed rather than germ tubes. Factors thought to influence the type of germination of basidiospores of the conifer rusts include pretreatment of basidiospores (Reed and Crabill 1915 and Spaulding and Rathbun-Gravatt 1926) and environmental conditions during germination (Bega 1960 and Hirt 1935); these did not enter into my experimental results, as conditions during germination tests were held constant and there was no pretreatment of basidiospores.

SUMMARY AND CONCLUSIONS

The rust fungus *Cronartium comandrae* was studied in the laboratory and field to determine how various environmental factors influence the rate of spread of comandra blister rust. *C. comandrae* overwinters and is perennial in cankers in pines. It dies out annually on comandra in the mountains. Activity of *C. comandrae* is thus limited chiefly to the growing season of the hosts.

Aeciospores that form on infected pines are disseminated by wind and infect only comandra plants. Aeciospores may survive several days of fairly severe conditions before losing viability; they germinate when exposed to mild temperatures on moist surfaces. Temperatures from 8° to 18° C. are best for maximum germination and germ tube growth. On comandra, germ tubes develop appressoria, which attach to stomates. From appressoria, infection pegs penetrate between guard cells to infect the plant. Maximum infection occurred in shoots held at 18° C. in mist chambers for 48 hours.

In the field, uredinia develop on comandra leaves and stems about 2 or 3 weeks after infection. By wind dispersal, urediniospores are distributed to other comandra shoots. Urediniospores also retain viability for several days after dissemination even under harsh conditions. In the presence of free water and mild temperatures, urediniospores germinate. Temperatures of about 13° to 23° C. are most favorable for germination and infection of comandra. Like those of aeciospores, germ tubes of urediniospores penetrate through stomates of comandra.

About 4 to 6 weeks after initial infection in the field, telia form on leaves and stems. The telia remain attached to comandra, and only under proper conditions do their teliospores germinate to form basidiospores that are dispersed by wind to infect pines. Teliospores germinate in either darkness or light after exposure to several hours of saturated air at mild temperatures. In unsaturated air telia may remain viable for several weeks. Prolonged exposure to temperatures above 25° C. reduces telial viability, and daily warm temperatures in the mountains probably reduce viability slowly. Freezing temperatures reduce telial viability. After about 6 hours' exposure to conditions favorable to germination, teliospores

begin casting basidiospores. The rate of casting is rapid for about 24 more hours if conditions remain favorable. Teliospores germinate over a range of temperatures of 6° to 24° C., but do best at temperatures from 13° to 23° C.

Basidiospores are easily injured by desiccation. Because they are delicate, effective dissemination of basidiospores is probably limited to only a few miles. Best germination occurs at about 13° to 23° C. Basidiospores derived from fresh telia germinate by means of germ tubes, but those from old telia more frequently form secondary basidiospores. Thus, fresh young telia are probably more effective inoculum for pines. Infection of pines occurs in needle-bearing shoots, but the means and exact site of infection are still unknown. Maximum infection in greenhouse trials occurred in seedlings held 48 hours in mist chambers at 20° C.

Outbreaks of comandra blister rust in lodgepole pine occur only rarely in the Rocky Mountain States because the complex series of climatic and biological events necessary for large-scale infection are seldom satisfied. An abundance of aecial inoculum during rainy June weather results in abundant infection of comandra in most years. Thundershowers in July and August tend to intensify infection by means of uredinia, so that comandra plants near lodgepole pine stands infected with comandra rust generally become heavily infected with this rust. However, despite the presence of large masses of telial inoculum, infection of pine usually does not occur because summer and early autumn weather does not permit it. Thundershowers sometimes provide conditions satisfactory for production and perhaps short-range dissemination of basidiospores, but conditions seldom remain favorable long enough for infection of pines. Extensive outbreaks of pine infection probably occur only when large warm frontal rains invade and remain in the region for several days during summers when there is an abundance of highly viable telial inoculum. Fortunately, this seldom happens in the Rocky Mountain States. By autumn, viable telial inoculum is less plentiful and though frontal storms are more frequent, prevailing temperatures are usually too cool for successful pine infection. While these studies point out the reasons for infrequent outbreaks of comandra rust in lodgepole pine, experience reminds us that when mass infection does occur, damage continues for many years over large areas.

LITERATURE CITED

Adams, J. F.
1919. Rusts on conifers in Pennsylvania. Penn. State Coll. Agr. Exp. Sta. Bull. 160:3-30.

Anderson, Neil Albert.
1960. Studies on the effects of the Cronartium rusts on jack pine and the epidemiology of these rusts. Diss. Abstr. 21:721.

Andrews, E. A., Gloria Rall, and Paul Lupcho.
1963. Infection of *Pinus contorta* by basidiospores of *Cronartium comandrae*. (Abstr.) Phytopathology 53:870.

Arthur, J. C.
1929. The plant rusts (Uredinales). 446 pp. New York: John Wiley and Sons.

Bega, R. V.
1960. The effect of environment on germination of sporidia in *Cronartium ribicola*. Phytopathology 50:61-69.

Duncan, D. B.
1955. Multiple range and multiple F tests. Biometrics 11:1-42.

Hedgcock, George G., and N. Rex Hunt.
1920. Notes on *Peridermium harknessii*. Phytopathology 10:395-397.

Hedgcock, George G., and William H. Long.
1915. A disease of pines caused by *Cronartium pyriforme*. U. S. Dep. Agr. Bull. 247, 20 pp.

Hirst, J. M.
1952. An automatic volumetric spore trap. Ann. Appl. Biol. 39:257-265.

Hirt, Ray R.
1935. Observations on the production and germination of sporidia of *Cronartium ribicola*. N.Y. State Coll. Forest. Tech. Pub. 46, 25 pp.

Hungerford, Kenneth E.
1957. A portable instrument shelter for ecological studies. Ecology 38:150-151.

Kimmey, James W.
1958. Forest diseases in multiple-use management in western United States. Soc. Amer. Forest. Proc. 1958:74-77.

Krebill, R. G.
1965. Comandra rust outbreaks in lodgepole pine. J. Forest. 63:519-522.

Laycock, W. A., and R. G. Krebill.
1967. Comandra, grazing, and comandra blister rust. U.S. Forest Serv. Res. Pap. INT-36, 9 pp.

MacLachlan, J. D.
1935. The dispersal of viable basidiospores of the Gymnosporangium rusts. J. Arnold Arboretum 26:411-422.

Mains, E. B.
1916. Some factors concerned in the germination of rust spores. Mich. Acad. Sci. Rep. 17:136-140.

Meinecke, E. P.
1928. The evaluation of loss from killing diseases in the young forest. J. Forest. 26:283-298.

Meinecke, E. P.
1929. Experiments with repeating pine rusts. Phytopathology 19:327-342.

Mielke, James L.
1957. The comandra blister rust in lodgepole pine. U.S. Forest Serv., Intermountain Forest and Range Exp. Sta. Res. Note 46, 8 pp.

Mielke, James L.
1961. Comandra blister rust. U.S. Dep. Agr., Forest Serv., Forest Pest Leaflet 62, 7 pp.

Patton, R. F.
1962. Inoculation with *Cronartium ribicola* by bark-patch grafting. Phytopathology 52:1149-1153.

Peterson, Roger S.
1962. Comandra blister rust in the central Rocky Mountains. U.S. Forest Serv., Rocky Mountain Forest and Range Exp. Sta. Res. Note 79, 6 pp.

Powell, J. M.
1965. Studies on forest tree rusts in Alberta. IN Canada Dep. Forest. Ann. Rep. Forest Entomol. and Pathol. Br., Year Ended March 31, 1965, pp. 129-130.

Reed, H. S., and C. H. Crabill.
1915. The cedar rust disease of apples caused by *Gymnosporangium juniperi–Virginianae* Schw. Virginia Agr. Exp. Sta. Tech. Bull. 9, 106 pp.

Riker, A. J., and Regina S. Riker.
1936. Introduction to research on plant diseases. John S. Swift Co., Inc. 117 pp.

Scharpf, Robert F.
1964. A compact system for humidity control. Plant Dis. Reptr. 48:66-67.

Spaulding, Perley, and Annie Rathbun-Gravatt.
1926. The influence of physical factors on the viability of sporidia of *Cronartium ribicola* Fischer. J. Agr. Res. 33:397-433.

Van Arsdel, E. P., A. J. Riker, and R. F. Patton.
1956. The effects of temperature and moisture on the spread of white pine blister rust. Phytopathology 46:307-318.

Winston, Paul W., and Donald H. Bates.
1960. Saturated solutions for the control of humidity in biological research. Ecology 41:232-237.

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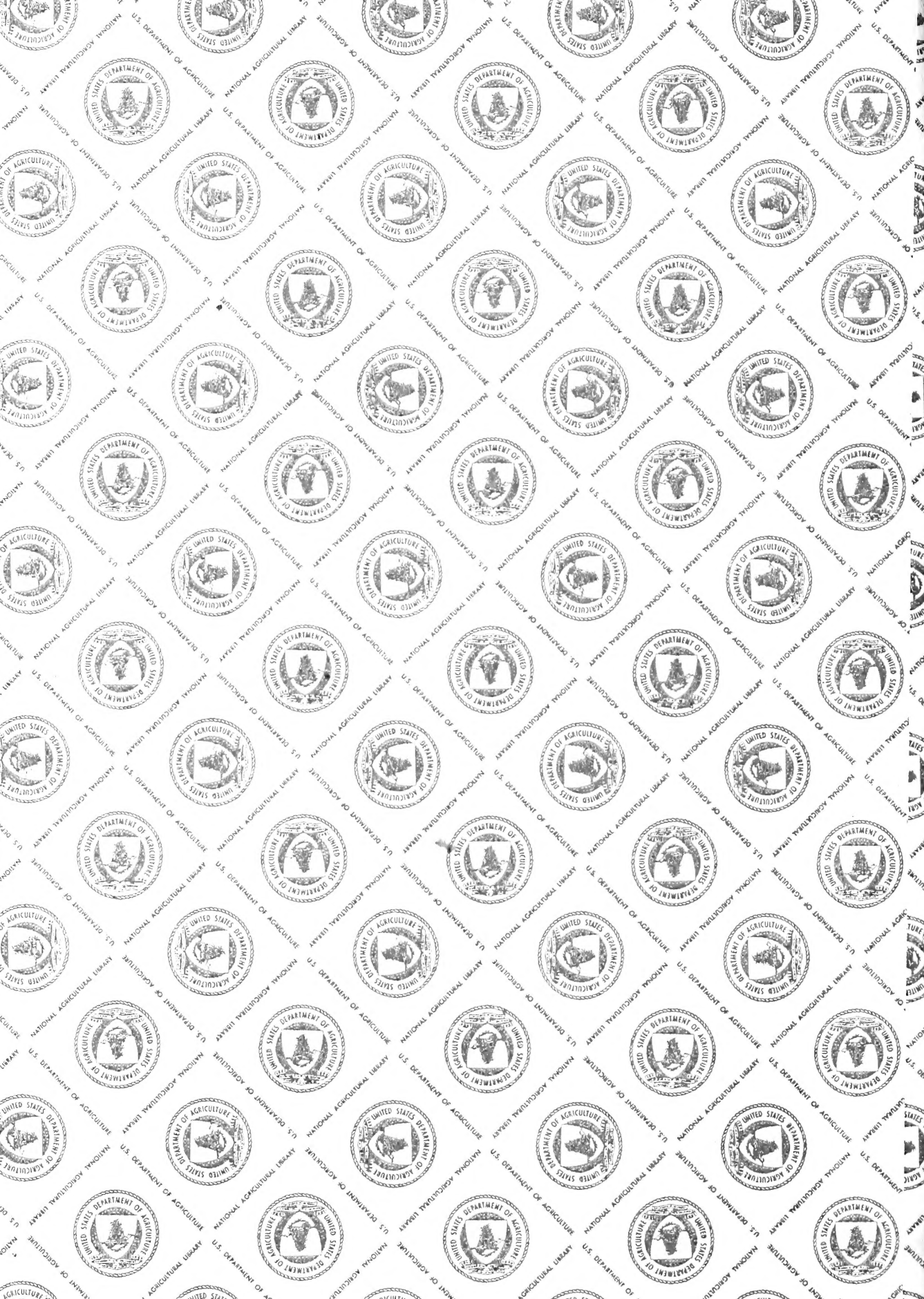
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